VESICULAR_ARBUSCULOR MYCORRHAZAE

OF Weedy and colonizer of Plant Species

at Disturbed Sites in Utah

VESICULAR-ARBUSCULAR MYCORRHIZAE OF WEEDY AND COLONIZER PLANT SPECIES AT DISTURBED SITES IN UTAH*

R. L. Pendleton and B.N. Smith

Department of Botany and Range Science

Brigham Young University

Provo, Utah 84602, USA

*This research supported by U.S. Department of Agriculture Forest Service, Intermountain Forest and Range Experiment Station, Agreement 12-11-204-31, Supplement No. 25.

SUMMARY

A survey was made of weedy species found on disturbed sites in Utah. Of the 74 species sampled, 57% were found to contain VA mycorrhizae. Mycorrhizal and nonmycorrhizal species strictly followed taxonomic divisions, regardless of growth habit. Nonmycorrhizal species were members of the Amaranthaceae, Brassicaceae, Capparidaceae, Caryophyllaceae, Chenopodiaceae, Papaveraceae, Polygonaceae, Portulacaceae, Rubiaceae, and Zygophyllaceae.

Cover data were obtained for all plant species colonizing seven of the disturbed sites. Flat semiarid sites were dominated by nonmycorrhizal species. The proportion of mycorrhizal plant cover increased with water availability. Rocky, sloping sites were dominated by mycorrhizal species. Deeply penetrating root systems may be necessary for seedling survival under conditions of extreme rockiness or slope. Disturbance by fire did not cause a significant change in the mycorrhizal component of the community.

INTRODUCTION

The majority of vascular plant species form some kind of mycorrhizal association. Vesicular-arbuscular (VA) mycorrhiza is the most commonly occurring form of mycorrhizae (Gerdemann 1975). The widespread occurrence of this type of association and enhanced growth which frequently accompanies it have led many workers to speculate on the necessity of VA mycorrhizae in natural communities (Janos 1980, Miller 1979, Reeves et al 1979). However, many species have been identified which rarely, if ever, form such an association.

Two hypotheses concerning the distribution of mycorrhizal and nonmycorrhizal species have been proposed. First, nonmycorrhizal plant species are taxonomically related. Early workers noted that nonmycorrhizal species are confined to certain family groups. A list of families which tend to be nonmycorrhizal was compiled in a 1968 review by Gerdemann. Since that time, other families have been examined which appear to be nonmycorrhizal (Khan 1974, 1978). Although the division of plant families into mycorrhizal and nonmycorrhizal groups is useful as a general rule, Gerdemann (1975) noted that the number of exceptions will likely increase as more species are examined.

Second, the distribution of mycorrhizal and nonmycorrhizal plants may be related to successional stages within the community. Recent studies by Reeves et al (1979) and by Miller (1979) suggest that under arid conditions, colonizers of disturbed soils tend to be nonmycorrhizal. Allen and Allen (1980) found that five of seven annuals growing on strip-mined and disked prairie sites were

nonmycorrhizal. Disturbance of soils reduces the number of mycorrhizal propagules (Moorman and Reeves 1979, Powell 1980). Reeves et al (1979) hypothesized that, under conditions of low soil inoculum, the "adaptative superiority of the invader plants is the ability to live without mycorrhizal fungi."

In the previously mentioned studies, nonmycorrhizal species found on the disturbed sites were members of the Chenopodiaceae, Brassicaceae, Polygonaceae, and Amaranthaceae. These families, traditionally considered nonmycorrhizal (Gerdemann 1968), contain a high percentage of weedy species. Miller (1979) suggests that the weedy growth habit or ruderal strategy is related to a plant's ability to do well without mycorrhizae. A weed is "a plant that grows spontaneously in a habitat that has been greatly modified by human action, and especially a species chiefly or wholly confined to such habitats" (Harper 1944 as cited in Curtis 1959). This study was undertaken to test the hypothesis that weedy species are predominantly nonmycorrhizal, regardless of family association. A second objective of the study was to determine the mycorrhizal status of colonizing species under various conditions of disturbance.

MATERIALS AND METHODS

A survey was made of the weedy plant species found on a variety of disturbed sites in Utah. The surveyed sites consisted of roadsides, roadcuts, vacant fields, graded lots, pinyon-juniper areas which had been chained, gravel pits, and burned portions of rangeland. Only those species which are designated in the species

descriptions as weedy or which grow primarily in disturbed habitats were included in the survey.

Roots were collected from a minimum of three plants per species and fixed in a standard formalin-acetic acid-alcohol (FAA) solution. Samples were cleaned and stained for the assessment of mycorrhizal colonization using the technique of Phillips and Hayman (1970). Arbuscules were observed in all species assigned a positive mycorrhizal status.

Seven disturbed sites were chosen for a study of all colonizing species. The sites were sampled in the spring and fall of 1981. In June, a list was made of the plant species colonizing each site. Root samples were collected from each species and returned to the lab for the assessment of mycorrhizal fungi. The sites were revisited in September. Any plant species not previously collected was identified and sampled. Percent cover of the colonizing species was measured using 1/4 m^2 quadrats. Thirty-five to 65 quadrats per site were taken 4 m apart along parallel transects. Cover data for the West Mountain burn was provided by Dr. Jack Brotherson, professor of Range Science at Brigham Young University. No cover data was taken at the Provo Canyon site due to the extreme steepness of the slope. An estimate of cover was made for the major species at this location. Site locations and descriptions are given below. Precipitation and temperature data were taken from the 1979 annual summary of Climatological Data, Utah.[1]

---

[1]U.S. Dept. Comm., Nat. Oceanic and Atmospheric Admin.

Gunnison, T19S, R1E, S20; elevation 1550 m. Annual precipitation 0.21 m; annual temperature 8.6 °C. The site is a level play area adjacent to the Gunnison Valley Elementary School. The area was originally graded 20 years ago and is now mown several times a year to a height of 0.08 m.

Circleville. T30S, R4W, S26; elevation 1850 m. Annual precipitation 0.17 m; annual temperature 8.4 °C. This graded, vacant lot was seeded with grass several years ago. The attempt failed. Vegetation is mown periodically to a height of 0.13 m.

Provo. T7S, R3E, S6; elevation 1390 m. Annual precipitation 0.25 m; annual temperature 11.3 °C. In 1979, pavement was removed and the area graded. The site was harrowed in June and regraded in July 1981.

Sheep Creek, Spanish Fork Canyon. T10S, R5E; elevation 1740 m. Annual precipitation 0.46 m; annual temperature[2] 10.9 °C. Originally a road base gravel source, this area was smoothed and reseeded in the fall of 1980. The slope is 43%.

---

[2]Station located 12 km west of the site at an elevation of 1440 m.

Panguitch. T35S, R5W, S11; elevation 2040 m. Annual precipitation 0.25 m; annual temperature 6.4 °C. This site consists of a gravel pit which has been in use for at least 9 years. The slope is 17%.

Provo Canyon. T5S, R3E, S13; elevation 1620 m. Annual precipitation 0.54 m; annual temperature 6.3 °C. The site is a roadcut made 20 years ago. The steep slope of 104% continually sloughs off rock and soil material.

West Mountain. T8S, R1E, S10,15; elevation 1500 to 1600 m. Annual precipitation 0.46 m; annual temperature 10.9 °C. Originally a sage-grass community, the site was severely burned in 1977. Vegetation in now dominated by annuals.

RESULTS

A list of the weedy plant species sampled and their mycorrhizal status in given in Table 1. Of the 75 species sampled, 42 species (56%) were found to contain VA mycorrhizae. No mycorrhizal structures were observed in the other 33 species. Species in which no structures were observed will be referred to as nonmycorrhizal, although we recognize that a sample may not reflect the normal status of the species (Trappe 1981).

Nonmycorrhizal species are members of the following families; Amaranthaceae*, Brassicaceae*, Capparidaceae, Caryophyllaceae*, Chenopodiaceae*, Papaveraceae, Polygonaceae*, Portulacaceae*, Rubiaceae, and Zygophyllaceae. The asterisk identifies families

listed as predominantly nonmycorrhizal in Gerdemann's (1968) review. Since that time, species in the Capparidaceae and Zygophyllaceae have been examined and found to be nonmycorrhizal (Khan 1974, Trappe 1981). Papaveraceae and Rubiaceae have not been extensively examined.

The degree of mycorrhizal infection varied greatly between plant species. For some species, mycorrhizal status was not consistent. In Ranunculus testiculatus, only three of six plant roots sampled from one location contained the endophyte. Root samples of Bromus tectorum, which is mycorrhizal under most conditions, did not contain VA fungi when growing exclusively with nonmycorrhizal species. Root infection of Guara parviflora and Lappula redowski was constantly lighter and more patchy than those of adjacent species. Patchy or inconsistent infection may indicate facultative species (Trappe, personal communication). In contrast, roots of Lactuca serriola, Tragopogon dubius, and Melilotus officinalis were heavily infected in most instances.

The seven study sites differed in the type of disturbance, length of time since disturbance, and in physical characteristics such as precipitation and slope. The proportion of mycorrhizal to nonmycorrhizal species invading the sites varied greatly.

Three of the sites consist of flat, graded lots located within the towns of Gunnison, Circleville, and Provo. These sites are dominated by nonmycorrhizal species. Fall vegetation cover on the Gunnison site was composed of two nonmycorrhizal species, Kochia scoparia and Halogeton glomeratus (Table 2). Spring vegetation

consisted of Bromus tectorum, Chorispora tenella, Lepidium perfoliatum, and Salsola kali, all of which were nonmycorrhizal. Although Bromus tectorum was infected at other locations, no VA structures were observed in root samples from this location. The prevalence of nonmycorrhizal colonizers on semiarid and arid disturbed sites has previously been noted (Reeves et al 1979, Miller 1979).

At Circleville, mycorrhizal species comprised only 0.4% of the total cover over most of the site (Circleville typical, Table 2). Where runoff from adjacent areas collected in a low corner of the field, however, the vegetation was markedly different. Plant species growing in the low area included Lactuca serriola, Bouteloua simplex, Iva axillaris, Agropyron smithii, Sporobolus cryptandrus, Distichlis stricta, and Lepidium perfoliatum. Plant cover in this area was 79.9% mycorrhizal (Circleville atypical, Table 2).

Despite repeated disturbance, the proportion of mycorrhizal species colonizing the Provo site was greater than that of the previous two sites. Total vegetation cover on the Provo site was 54.6%; 23.7% for mycorrhizal species and 30.9% for nonmycorrhizal species. Higher precipitation at this site likely contributes to the shift toward mycorrhizal species.

The Sheep Creek, Panguitch, and Provo Canyon sites were characterized by rocky or gravelly slopes and sparse vegetation. The dominant plant species were found to be mycorrhizal (Table 2). At Sheep Creek, seven of nine species and 87% of the total plant cover was mycorrhizal. At Panguitch, six of eight species and 74% of the total cover was mycorrhizal. At the Provo Canyon site, nine

of eleven species and approximately 98% of the cover was mycorrhizal. Studies by Daft (1974), Nicolson (1960), and Khan (1978) document instances in which the majority of colonizing species were mycorrhizal. Samples of Melilotus officinalis and Melilotus alba collected from the Sheep Creek and Provo Canyon sites were nodulated with nitrogen-fixing bacteria. Harley (1970) noted that plants with dual symbiotic relationships, mycorrhizal and nitrogen fixing, should have an advantage in colonizing areas of low nutrient availability.

Colonizers of this second group of sites were, in addition to being mycorrhizal, primarily species with deep, tough root systems. Shrubs and half-shrubs with their deep rooting patterns are reportedly better adapted to rocky soils than grasses (Jensen et al 1979). Plant species which lack a deep root system such as Kochia scoparia, Bromus tectorum, and Veronica biloba were concentrated at the base of the slope. Under conditions of unstable and rocky slopes, a deeply penetrating root system may be necessary for seedling establishment and survival. The exception appears to be Salsola kali, which has been observed colonizing fairly steep slopes.

Disturbance by fire apparently causes little change in the mycorrhizal component of the community. Vegetation at the West Mountain site was dominated by annual weeds on the burned portion of rangeland and by a sage-grass community on the adjacent unburned portion. Despite the difference in species composition of the two areas, the percent cover of mycorrhizal species was approximately equal (West Mountain, Table 2). Initial damage by fire to soil

microflora was probably limited to the upper 0.05 cm or less. Dunn and DeBano (1977) found that the maximum temperature tolerated by fungi in dry soil was 155 °C. Maximum soil temperatures recorded for a California brush fire were 166 °C at 0.025 m depth and 66 °C at a 0.05 m depth (DeBano and Rice 1971). Spores and infected roots present below the lethal point should provide an ample source of inoculum for young seedlings. Tarrant (1956) found that colonization of Douglas-fir seedlings by ectomycorrhizal fungi was 79% recovered the second year following a burn.

DISCUSSION

Contrary to the original hypothesis, over half of the weedy species examined did contain the endophyte. The presence or absence of mycorrhizal fungi in plant species strictly followed taxonomic divisions. It appears that family connection is much more important than weedy habit in determining the mycorrhizal status of a species. Stebbins (1965), speaking of the relationship between polyploidy and weediness, remarked, "where there is polyploidy there is a correlation between polyploidy and weediness, but where there isn't polyploidy you can still get weeds." The same might be said for plant groups which are nonmycorrhizal. Weedy species are common in nonmycorrhizal families such as the Amaranthaceae, Brassicaceae, and Chenopodiaceae, but species from mycorrhizal families may also become weeds.

The patchy infection pattern of roots of *Guara parviflora* and the inconsistency between individual samples of *Bromus tectorum* and *Ranunculus testiculatus* indicate that a few species designated here

as mycorrhizal may be facultative in their dependence on the association. Piemeisel (1938) documented succession on cleared sagebrush land from Salsola kali to Descurainia pinnata or Sisymbrium altissimum to Bromus tectorum, a change of nonmycorrhizal species to a probable facultative species. Increase of disturbance pressure caused regression to Salsola kali (Young et al 1972). Once established, facultative species should provide a host for wind-blown spores of VA fungi and allow the soil inoculum to build.

The mycorrhizal status of plant species which colonize a disturbed site depends on many factors. Colonizers of severely disturbed habitats have been characterized as predominantly mycorrhizal (Daft and Nicolson 1974, Khan 1978) or predominantly nonmycorrhizal (Miller 1979, Reeves et al 1979). Several attributes have been described which can preadapt a plant towards becoming a colonizer (Baker 1965, Harper 1965). Lack of dependence on mycorrhizal fungi may be advantageous to colonizers under certain circumstances, but little is known about conditions for which this is true.

Our studies suggest that degree of disturbance, precipitation, and slope may be some of the important factors influencing the type of species, mycorrhizal or nonmycorrhizal, which colonize a site. In the case of fire, the degree and type of disturbance was insufficient to cause a significant change in the mycorrhizal component of the community. Of the severely disturbed sites, flat semiarid sites were dominated by nonmycorrhizal species. Water availability seemed extremely important on these sites in determining the number and proportion of mycorrhizal colonizers.

The rocky sloped sites were dominated by mycorrhizal species. Deeply penetrating root systems appear advantageous to colonizers of these rocky slopes. Precipitation was less important in steep sites than on flat sites.

Our data strongly uphold previous observations that nonmycorrhizal species are taxonomically related. That is, certain families possess some characteristic, morphologic or physiologic, which inhibits the formation of mycorrhizal associations. A weedy growth habit is not strongly linked to the nonmycorrhizal state. The data weakly support the hypothesis that mycorrhizal species increase with successional stages within the community. This hypothesis holds true for flat semiarid sites. However, colonizers which form mycorrhizal associations predominate on sites having a rocky matrix or steep slope.

REFERENCES

Allen EB and Allen MF (1980) Natural re-establishment of vesicular arbuscular mycorrhizae following stripmine reclamation in Wyoming. J Appl Ecol 17:139-147.

Baker HG (1965) Characteristics and modes of origin of weeds. In: HG Baker and GL Stebbins (eds), The Genetics of Colonizing Species, p 147-168 Academic Press, New York.

Curtis JT (1959) The Vegetation of Wisconsin, University of Wisconsin Press, Madison, Wisconsin. 657 p.

Daft MJ and Nicolson TH (1974) Arbuscular mycorrhizas in plants colonizing coal wastes in Scotland. New Phytol 73;1129-1138.

DeBano LF and Rice RM (1971) Fire in vegetation management - its effect on soil. In: Proc Interdisciplinary aspects of watershed management: A symposium. Bozeman, Montana, August 3, 1971:327-346.

Dunn PH and DeBano LF (1977) Fire's effect on the biological and chemical properties of chaparral coils. In: Interdisciplinary symposium on the environmental consequences of fire and fuel management in Mediterranean climate ecosystems (Palo Alto, California; August 1-5, 1977), p 75-84 US Department of Agriculture Forest Service Gen Tech Rep, WO-3, 498p.

Enrendorfer F (1965) Dispersal mechanisms, genetic systems, and colonizing abilities in some flowering plant families. In: HG Baker and GL Stebbins (eds), The Genetics of Colonizing Species, p 331-351, Academic Press, New York.

Gerdemann JW (1968) Vesicular-arbuscular mycorrhiza and plant growth. Ann Rev Phytopathol 6:397-418.

Gerdemann JW (1975) Vesicular-arbuscular mycorrhizae. In: JR Torrey and DT Clarkson (eds), The Development and Function of Roots, p 575-591, Academic Press, London.

Harley JL (1970) The importance of micro-organisms to colonizing plants. Trans Bot Soc Edinburgh 41:65-70.

Harper JL (1965) Establishment, aggression, and cohabitation in weedy species. In: HG Baker and GL Stebbins (eds), The Genetics of Colonizing Species, p 243-265, Academic Press, New York.

Janos DP (1980) Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth Ecology 61:151-162.

Jensen IB and Sindelar BW (1979) Permanent stabilization of semiarid roadsides with grass, legume, and shrub seed mixtures and native grass dryland sodding. US Department of Agriculture Forest Service Res Rep 141(3);34 p.

Khan AG (1978) Vesicular-arbuscular mycorrhizae in plants colonizing black wastes from bituminous coal mining in the Illawarra region of New South Wales. New Phytol 81:57-63.

Khan AG (1974) The occurrence of mycorrhizas in halophytes, hydrophytes, and xerophytes, and of Endogone spores in adjacent soils. J Gen Microbiol 81:7-14.

Miller RM (1979) Some occurrences of vesicular-arbuscular mycorrhiza in natural and disturbed ecosystems of the Red Desert. Can J Bot 57:619-623.

Moorman T and Reeves FB (1979) The role of endomycorrhizae in revegetation practices in the semi-arid West. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. Am J Bot 66:14-18.

Nicolson TH (1960) Mycorrhiza in the Gramineae. II. Development of different habitats, particularly sand dunes. Trans Br Mycol Soc.43:132-145.

Phillips JM and Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans Br Mycol Soc 55:158-160.

Piemeisel RL (1938) Changes in weedy plant cover on cleared sagebrush land and their probable causes. US Department of Agriculture Tech Bull 654, 48 p.

Powell CL (1979) Mycorrhizal infectivity of eroded soils. Soil Biol Biochem 12:247-250.

Reeves FB, Wagner D, Moorman T, and Kiel J (1979) The role of endomycorrhizae in revegetation practices in the semi-arid West. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. Am J Bot 66:6-13.

Stebbins LG (1965) Discussion of paper by Dr. Stebbins. In: HG Baker and GL Stebbins (eds), The Genetics of Colonizing Species, p 192-195, Academic Press, New York.

Tarrant RF (1956) Effects of slash burning on some soils of the Douglas-fir region. Soil Sci Soc Am Proc 20:408-411.

Trappe JM (1981) Mycorrhizae and productivity of arid and semiarid rangelands. In: J Manassah and EJ Briskey (eds) Advances in Food Producing Systems for Arid and Semi Arid Lands, p 581-599, Academic Press, New York.

Young JA, Evans RA, and Major J (1972) Alien plants in the Great Basin. J Range Manage 25:194-201

Table 1. Mycorrhizal status of weedy plant species collected from disturbed sites in Utah

Plant Species	Mycorrhizal Status[1]	Plant Species	Mycorrhizal Status
*AMARANTHACEAE[2]		*CHENOPODIACEAE	
Amaranthus graecizans	-	Atriplex rosea	-
ASCLEPIADACEAE		Chenopodium album	-
Asclepias speciosa	+	Halogeton glomeratus	-
ASTERACEAE		Kochia scoparia	-
Ambrosia acanthicarpa	+	Salsola kali	-
Ambrosia psilostachya	+	CONVOLVULACEAE	
Carduus nutans	+	Convolvulus arvensis	+
Conyza canadensis	+	EUPHORBIACEAE	
Grindelia squarrosa	+	Euphorbia glyptosperma	+
Helianthus annuus	+	FABACEAE	
Iva axillaris	+	Medicago lupulina	+
Lactuca serriola	+	Melilotus alba	+
Matricaria matricarioides	+	Melilotus officinalis	+
Senecio vulgaris	+	GERANIACEAE	
Sonchus asper	+	Erodium cicutarium	+
Taraxacum officinale	+	LAMIACEAE	
Tragopogon dubius	+	Lamium amplexicaule	+
BORAGINACEAE		MALVACEAE	
Amsinckia retrorsa	+	Malva neglecta	+
Cynoglossum officinale	+	ONAGRACEAE	
Lappula redowskii	+	Gaura parviflora	+
*BRASSICACEAE		OXALIDACEAE	
Alyssum allyssoides	-	Oxalis stricta	+
Alyssum desertorum	-	PAPAVERACEAE	
Brassica kaber	-	Argemone munita	-
Brassica nigra	-	PLANTAGINACEAE	
Camelina microcarpa	-	Plantago major	+
Capsella bursa-pastoris	-	POACEAE	
Cardaria draba	-	Bromus japonicus	+
Chorispora tenella	-	Dactylis glomerata	+
Descurainia pinnata	-	Digitaria ischaemum	+
Descurainia sophia	-	Hordeum jubatum	+
Euclidium syriacum	-	Poa bulbosa	+
Isatis tinctoria	-	Setaria viridis	+
Lepidium campestre	-	*POLYGONACEAE	
Lepidium perfoliatum	-	Eriogonum cernuum	-
Malcolmia africana	-	Polygonum aviculare	-
Sisymbrium altissimum	-	Polygonum convolvulus	-
*CARYOPHYLLACEAE		Rumex crispus	-
Holosteum umbellatum	-	*PORTULACACEAE	
CAPPARIDACEAE		Portulaca oleraceae	-
Cleome lutea	-	RANUNCULACEAE	
Cleome serrulata	-	Ranunculus testiculatus	+
		RUBIACEAE	
		Galium aparine	-

Table 1 (continued)

SCROPHULARIACEAE		VERBENACEAE	
Linaria dalmatica	+	Verbena bracteata	+
Linaria vulgaris	+	ZYGOPHYLLACEAE	
Verbascum thapsus	+	Tribulus terrestris	–
Veronica biloba	+		
Veronica persica	+		

[1] + = VA mycorrhizae present; – = VA mycorrhizae absent

[2] * = Families generally considered nonmycorrhizal

Table 2. Mycorrhizal status and percent cover of plant species colonizing seven disturbed sites

Location	Species	%Mean Ground cover	Mycorrhizal status
Gunnison	Halogeton glomeratus	0.01	−
	Kochia scoparia	18.28	−
Circleville (typical)	Bromus tectorum	0.01	+
	Descurainia sophia	1.88	−
	Grindelia squarrosa	0.13	+
	Kochia scoparia	36.79	−
	Malva neglecta	0.04	+
	Polygonum aviculare	2.96	−
	Salsola kali	0.07	−
Circleville (atypical)	Agropyron smithii	15.88	+
	Bouteloua simplex	1.03	+
	Bromus tectorum	.15	+
	Descurainia sophia	.06	−
	Distichlis stricta	3.09	+
	Grindelia squarrosa	13.38	+
	Iva axillaris	1.21	+
	Kochia scoparia	5.53	−
	Lactuca serriola	0.88	+
	Lepidium perfoliatum	0.15	−
	Polygonum aviculare	3.26	−
	Sporobolus cryptandrus	0.15	+
Provo	Amaranthus graecizans	0.09	−
	Chenopodium album	0.05	−
	Chenopodium blaucum	0.36	−
	Convolvulus arvensis	1.25	+
	Digitaria ischaemum	0.46	+
	Erodium cicutarium	0.11	+
	Euphorbia glyptosperma	2.46	+
	Lactuca serriola	0.95	+
	Malva neglecta	14.78	−
	Melilotus officinalis	0.05	+
	Poa pratensis	2.01	+
	Polygonum aviculara	3.72	−
	Portulaca oleracea	1.63	−
	Setaria viridis	1.61	+
	Tragopogon dubius	0.01	+
	Tribulus terrestris	24.27	−
	Verbena bracteata	0.05	+

Table 2 (continued)

Sheep Creek	Bromus tectorum	0.04	+
	Carduus nutans	0.96	+
	Grass (seeded)	0.15	+
	Iva axillaris	0.01	+
	Melilotus officinalis	7.99	+
	Mentzelia laevicaulis	0.27	–
	Oryzopsis hymenoides	0.04	+
	Salsola kali	1.38	–
	Verbascum thapsus	2.23	+
Panguitch	Astragalus geyeri	0.05	+
	Chrysothamnus nauseosus	9.68	+
	Cryptantha abata	0.27	+
	Kochia scoparia	3.19	–
	Salsola kali	0.38	–
	Sitanion hystrix	0.05	+
	Tragopogon dubius	0.01	+
	Verbascum thapsus	0.32	+
Provo Canyon[2]	Brassica nigra	0.01	–
	Helianthus annuus	0.04	+
	Lactuca serriola	0.04	+
	Linaria dalmatica	2.1	+
	Melilotus alba	0.9	+
	Mentzelia dispersa	0.1	–
	Nepeta cataria	0.6	+
	Verbascum thapsus	2.7	+
	Veronica biloba	0.1	+
West Mountain (burned)	Agropyron spicatum	0.1	+
	Artemisia dracunculus	0.1	+
	Asclepias speciosa	0.1	+
	Bromus japonicus	0.1	+
	Bromus tectorum	52.0	+
	Chrysothamnus viscidiflorus	0.1	+
	Erodium cicutarium	38.8	+
	Euphorbia sp.[3]	0.5	+
	Helianthus annuus	0.1	+
	Poa bulbosa	4.5	+
	Poa sandbergii	4.2	+
	Ranunculus testiculatus	0.1	+
	Sisymbrium altissimum	0.2	–
	Sporobolus cryptandrus	0.1	+
	Xanthocephalum sarothrae	1.0	+

[2] Cover data not collected due to steepness of the site.

[3] Study site reburned before this species could be collected and identified.

Table 2 (continued)

West Mountain (unburned)	Agropyron spicatum	37.8	+
	Alyssum alyssoides	0.9	−
	Artemisia tridentata	17.0	+
	Bromus tectorum	0.1	+
	Calochortus nuttallii	0.2	+
	Hedysaurum boreale	0.9	+
	Juniperus osteosperma	0.9	−(+)[4]
	Poa sandbergii	2.1	+
	Petradoria pumila	0.8	+

[4] Although the sample we collected did not contain the endophyte this species has been reported as mycorrizal (Reeves et al 1979).

STUDIES ON THE OCCURRENCE OF VESICULAR-ARBUSCULAR MYCORRHIZAE:

EXAMINATION OF NATURAL AND DISTURBED COMMUNITIES

OF UTAH AND THE COLORADO ROAN PLATEAU

Manuscripts of Three Journal Articles

Presented to the

Department of Botany and Range Science

Brigham Young University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Rosemary L. Pendleton

December 1981

ACKNOWLEDGMENTS

I would like to thank Dr. Neil C. Frischknecht, the U.S. Forest Service and the Intermountain Forest and Range Experiment Station Shrub Sciences Lab for providing the financial support and the opportunity to continue my education. I wish to thank Dr. Bruce N. Smith for his help in research design, manuscript organization and encouragement. Thanks to Dr. Darrell Weber, Dr. Kimball T. Harper and Dr. Richard Terry for their helpful suggestions and comments on the manuscripts. Sherel Goodrich, Kaye Thorne and Elizabeth Neese provided much needed aid in plant identification. Robert B. Ferguson, Dr. Dave Nelson, Dr. Jerran Flinders and Dr. Jack Brotherson have all provided valuable assistance at some point in the project. Special thanks go to Dr. James M. Trappe for the time spent in his lab studying slides of mycorrhizal fungi, and for his help in identifying the fungal species. I also wish to thank Burton Pendleton for his confidence in me and for his ideas and advice throughout the past two years.

This manuscript of Journal Articles, by Rosemary L. Pendleton, is accepted in its present form by the Department of Botany and Range Science of Brigham Young University as satisfying the thesis requirement for the degree of Master of Science.

Bruce N. Smith

Bruce N. Smith, Committee Chairman

Neil C. Frischknecht

Neil C. Frischknecht, Committee Member

Darrell Weber

Darrell J. Weber, Committee Member

Dec 14, 1981

Date

Wilford M. Hess

Wilford M. Hess, Graduate Coordinator

VESICULAR-ARBUSCULAR MYCORRHIZAL POPULATIONS AT COAL AND OIL SHALE SITES

R. L. Pendleton and N. C. Frischknecht

USFS Intermountain Forest and Range Experiment Station

Shrub Sciences Lab

735 North 500 East

Provo, Utah 84601 USA

[B.Y.U.]

ABSTRACT

The mycorrhizal status of dominant plant species growing at one oil shale and two coal field sites was determined. In all cases, the majority of species contained VA mycorrhizae. Soils collected from each site were screened for fungal spores. A total of seven species of VA fungi were isolated from the three locations.

A bioassay was used to determine the effects of three amendments to processed oil shale on soil inoculum potential. The inoculum potential of replaced topsoil was close to that of soil in the surrounding undisturbed community. Straw-mulched shale contained no viable inoculum. The addition of rock fragments to the shale surface greatly improved the inoculum potential.

INTRODUCTION

The association of a vesicular-arbuscular (VA) mycorrhizal fungus with a host plant root is known to increase plant growth and aid in the uptake of nutrients, particularly phosphorus. The presence of VA fungi seems to be essential in most ecosystems (Mosse 1973), and may be particularly important in the low-phosphate soils of the semiarid west (Moorman and Reeves 1979). Recent surveys of natural communities in western lands revealed a high incidence of mycorrhizal fungi in the dominant plant cover (Miller 1979, Molina et al 1978, Reeves et al 1979).

The establishment of mycorrhizal associations should be an important consideration in reestablishing native vegetational cover on reconstructed soils of coal and oil shale lands. Mine spoil material is generally low in fertility and plant cover is often difficult to establish (Bradshaw 1970, Schramm 1966). Once established, mycorrhizal plant species may have a competitive advantage over nonmycorrhizal species growing on mine spoil material. Several studies have shown the presence of mycorrhizal fungi in plants successfully colonizing coal mine spoils (Daft & Nicolson 1974, Khan 1978, Ponder 1979). Inoculation by VA fungi greatly improved survival and growth of shrubs grown in mine spoil material (Aldon 1975, Lindsey et al 1977).

Prior to mining, the role of VA mycorrhizae in the natural community should be established through extensive soil and vegetational sampling. The frequency and degree of mycorrhizal colonization is evaluated in root samples collected from the dominant plant species. Soils should be sampled to determine the type and relative amount of

fungal species present. The primary objective of this study was to evaluate the importance of VA fungi in natural communities of the Alton and Emery coal fields and an oil shale site located on the Colorado Roan Plateau.

Little work has been done on mycorrhizal aspects of processed oil shale reclamation. The processed material is low in nutrients, highly saline and completely sterile (Schmehl and McCaslin 1973). Inoculum must be added by use of soil amendments or through the planting of inoculated host plants. The second objective of this study was to determine the effect of various amendments to processed oil shale on soil inoculum potential.

MATERIALS AND METHODS

Study Areas

Three study areas chosen for assessment of mycorrhizal fungi were sampled during the summer of 1980. The first study area is a stripable coal field located near Alton, Utah. Native vegetation consists of interspersed pinyon-juniper and sagebrush communities. Soils were sampled from pinyon-juniper, sagebrush and sites where pinyon and juniper had been replaced with a grass-legume mixture. The vegetation was sampled at the sagebrush site.

The second study area is a stripable coal field located near Emery, Utah. The vegetation is dominated by species of *Artemisia*, *Atriplex* and desert grasses. Soils and vegetation were sampled from three sites at this location: clay bottom, sandy hillside and a shallow-soiled hilltop.

The third study area is located at Davis Gulch, on the oil shale lands of the Colorado Roan Plateau. Native vegetation is mountain brush interspersed with mid-elevation sagebrush. The vegetation and soil was sampled in the sagebrush community. Soils were also sampled from study plots set up at this location in 1976. Sampling was done in 1980 to determine the effect of soil amendments on soil infectivity. The four treatments sampled were:

1. Compacted processed oil shale, 76 cm deep, covered with 15 to 25 cm of native topsoil.
2. Compacted processed oil shale, 76 cm deep, covered with 3 to 10 cm of sandstone rock fragments obtained at the study site.
3. Compacted processed oil shale, 76 cm deep, with barley straw tilled into the top 15 cm at a rate of 4500 kg per hectare.
4. One meter of subsoil material only.

A list of soil properties for these treatments is found in Table 5.

Soil and Vegetation Survey

Soils were sampled to a depth of 15 cm using a soil auger. Three samples were taken near the base of each major plant species. Soil samples were screened for spores using the wet-sieve technique of Gerdemann (1955). Sievings collected between the 1 mm and 53 um sieves were examined for species of mycorrhizal fungi. Identification of these spores followed the Synoptic Key to the Endogonaceae (Trappe in preparation).

Root samples were taken from a minimum of three plants per species for the dominant species found at each study site. Root samples were fixed in a standard solution of formalin-acetic acid-alcohol (FAA).

The fixed root samples were then cleared and stained using the technique of Phillips and Hayman (1970). A positive mycorrhizal status was assigned to species in which arbuscules were observed.

Bioassay of Amendments to Processed Oil Shale

Soils were sampled from each of the four treatments to processed oil shale made at the Davis Gulch study site. Soil samples were taken to a depth of 15 cm at 2-m intervals along a 28-m transect. A total of 15 samples were taken from each treatment. The soil of the surrounding vegetation was sampled in the same manner. The samples from each soil type were composited, mixed and stored at $4^{o}C$.

The composited soil samples were bioassayed to determine the relative infectivity of each soil type (Moorman and Reeves 1979). Bioassays were run on undiluted soil and soils diluted 1:4 and 1:40 with a sterile mixture of 1:1:1 perlite, vermiculite and sand. Controls were made by autoclaving soil from each treatment for one hour at 15 psi. Sixty surface-sterilized pots were prepared for each of the soil treatments, 15 of which were filled with undiluted soil, 15 with soil diluted 1:4, 15 with soil diluted 1:40 and 15 with sterilized control soil. All pots were planted with one plant of subterranean clover. Proir to planting, subterranean clover seeds were surface sterilized in 10% sodium hypochlorite for 10 minutes and germinated on 3% water agar. Five plants each from control, undiluted and diluted soils of all treatments were harvested at 30-, 60- and 90-day intervals.

To assay for infection, roots were washed, cut into approximately 1 cm segments and stained according to Phillips and Hayman (1970). Percent colonization was determined using the adapted gridline-intersect

method of Ambler and Young (1977) as reviewed by Giovannetti and Mosse (1980).

RESULTS

Root samples from 11 plant species in 7 families were collected from the Alton coal field. A list of these species and their mycorrhizal status is given in Table 1. All species are mycorrhizal with the exception of Castilleja chromosa, a root parasite.

Twenty-five species in 10 families were collected from the Emery coal field. The mycorrhizal status of these species is given in Table 2. The majority of species are mycorrhizal. Arbuscules were observed in 15 species, hyphae and/or vesicles were observed in an additional 5 species. Nonmycorrhizal species are members of the Brassicaceae, Onagraceae and Polygonaceae.

Forty-two species in 18 families were collected from the oil shale site at Davis gulch. A list of these species and their mycorrhizal status is given in Table 3. Twenty-nine species (69%) are mycorrhizal. Nonmycorrhizal species are members of the Brassicaceae, Cactaceae, Capparidaceae, Cyperaceae, Loasaceae, Onagraceae, Polygonaceae, Primulaceae and Solanaceae.

Table 4 lists the species of mycorrhizal fungi identified from each study area. A total of seven species were isolated from the three study areas. Three species were isolated from the Alton coal field, five from the Emery coal field and three from Davis Gulch. Species of mycorrhizal fungi are often distributed on a world-wide basis. Many of the fungal species isolated from our study sites were also found on coal wastes in Wyoming (Allen & Allen 1980), Pennsylvania,

Scotland (Daft et al 1975) and Australia (Khan 1978). Glomus fasciculatus seems to occur most frequently.

A 30-day growth period gave the clearest results for determination of relative infectivity (Figure 1). Percent colonization of roots grown for this time period in undiluted soils were 72% for undisturbed topsoil, 55% for topsoil over shale, 43% for subsoil, 42% for the rock mulch treatment and 0% for the straw-mulched shale. As growth periods increased, colonization reached high levels and differences between treatments became less distinct.

Although topsoil was stockpiled for one year, inoculum potential remained high. The straw-mulched shale contained no inoculum although it was expected that during the four years since the plots were established, rain, wind or small rodents would have deposited spores on the shale surface. This suggests that processed shale may be too harsh of an environment to allow spore germination. The addition of rock fragments to the shale surface greatly improved the inoculum potential of the soil. Since it is unlikely that inoculum was present in the rock fragments, the addition of rock mulch may make conditions more favorable for transported spores to germinate.

The relative infectivity of the treatment soils is positively correlated with the number of species which had invaded onto the treatment plots (Figure 2). The correlation, using the Pearson Product-Moment Correlation Coefficient, was significant at the .025 level. A list of the invading plant species is given for each treatment in Appendix 1.

DISCUSSION

Mycorrhizal research in the western U.S. is quite recent. Many of the common plant species have not yet been examined for mycorrhizal associations. Surveys of the dominant vegetation on the Alton, Emery and Davis Gulch study sites revealed that the majority of plant species were mycorrhizal. Successful revegetation by native species must include the establishment of mycorrhizal associations.

Surface treatment of mined soils may affect the survival and persistence of mycorrhizal fungi. The addition of a rock mulch greatly improved inoculum potential over that of unamended processed shale. Stockpiled topsoil retains sufficient inoculum potential for at least one year.

Locally adapted species of mycorrhizal fungi should be used as the inoculum source for replacement vegetation. Evidence exists that fungal species differ in their ability to increase plant growth (Hirrel and Gerdemann 1980, Khan 1978). Fungal species are adapted to a specific range of soil conditions including light, pH and temperature (Green et al 1976, Lambert et al 1980). The use of inoculum species which are not adapted to existing soil conditions may reduce the success of reclamation.

LITERATURE CITED

Aldon, E.F. 1975. Endomycorrhizae enhance survival and growth of fourwing saltbush on coal mine spoils. USDA For. Serv. Res. Note RM-294. Rocky Mt. For. and Range Exp. Sta., Fort Collins, Colorado. 2 pp.

Allen, E.B. and M.F. Allen. 1980. Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. J. Appl. Ecol. 17:139-147.

Ambler, J.R. and J.L. Young. 1977. Techniques for determining root length infected by vesicular-arbuscular mycorrhizae. Soil Soc. Am. J. 41:551.

Bradshaw, A.D. 1970. Plants and industrial waste. Trans. Proc. Bot. Soc. Edinburgh 41:71.

Daft, M.J., E. Hacskaylo and T.H. Nicolson. 1975. Arbuscular mycorrhizas in plants colonizing coal spoils in Scotland and Pennsylvania. In F.E. Sanders, B. Mosse and P.B. Tinker (eds), Endomycorrhizas. Academic Press, London. p 561-580.

Daft, M.S. and T.H. Nicolson. 1974. Arbuscular mycorrhizas in plants colonizing coal wastes in Scotland. New Phytol. 73:1129-1138.

Gerdemann, J.W. 1955. Relation of a large soil-borne spore to Phycomycetous mycorrhizal infections. Mycologia 47:619-632.

Giovannetti, M. and B. Mosse. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. 84:489-500.

Green, N.E., S.O. Graham, and N.C. Schenck. 1976. The influence of pH on the germination of vesicular-arbuscular mycorrhizal spores. Mycologia 68:929-934.

Hirrel, M.C. and J.W. Gerdemann. 1980. Improved growth of onion and bell pepper in saline soils by two vesicular-arbuscular mycorrhizal fungi. Soil Sci. Soc. Am. J. 44:645-655.

Khan, A.G. 1978. Vesicular-arbuscular mycorrhizas in plants colonizing black wastes from bituminous coal mining in the Illawarra region of New South Wales. New Phytol. 81:57-63.

Lambert, D.H., H. Cole Jr., and D.E. Baker. 1980. Adaptation of vesicular-arbuscular mycorrhizae to edaphic factors. New Phytol. 85:513-520.

Lindsey, D.L., W.A. Cress, and E.F. Aldon. 1977. The effects of endomycorrhizae on the growth of rabbitbrush, four-wing saltbush, and corn in mine spoil material. USDA For. Serv. Res. Note RM-343. Rocky Mt. For. and Range Exp. Stal, Fort Collins, Colorado. 6 pp.

Miller, R.M. 1979. Some occurrences of vesicular-arbuscular mycorrhiza in natural and disturbed ecosystems of the Red Desert. Can. J. Bot. 57:619-623.

Molina, R.J., J.M. Trappe, and G.S. Strickler. 1978. Mycorrhizal fungi associated with Festuca in the western United States and Canada. Can. J. Bot. 56:1691-1695.

Moorman, T. and F.B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semiarid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. Am. J. Bot. 66:14-18.

Mosse, B. 1973. Advances in the study of vesicular-arbuscular mycorrhiza. Ann. Rev. Phytopathol. 11:171-190.

Phillips, J.M. and D.S. Hayman. 1970. Improved procedure for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Brit. Mycol. Soc. 55:158-160.

Ponder, F., Jr. 1979. Presence of endomycorrhizal fungi in recently graded coal mine spoil. J. Soil and Water Cons. 34:186-187.

Reeves, F.B., D. Wagner, T. Moorman, and J. Kiel. 1979. The role of endomycorrhizae in revegetation practices in the semiarid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. Am. J. Bot. 66:6-13.

Schmehl, W.R. and B.D. McCaslin. 1973. Some properties of spent oil shale significant to plant growth. In M. B. Blich and P.D. Kilburn (eds), Processed shale revegetation studies. Colony Development Operation, Denver, Colorado. p.7-25.

Schramm, J.R. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. Trans. Am. Phil. Soc. 47:331.

Table 1. Mycorrhizal status of plant species collected from a sagebrush community at the Alton coal field.

Plant Species	Mycorrhizal Status[1]
Artemisia nova	+
Artemisia tridentata	+
Astragalus sp.	+
Castilleja chromosa	-
Cymopterus purpureus	+
Chrysothamnus nauseosus	+
Leucocrinum montanum	+
Phlox longifolia	+
Sphaeralcea coccinea	+
Sphaeralcea parvifolia	+
Zygadenus paniculatus	+

[1] + = VA mycorrhizae present
- = VA mycorrhizae absent

Table 2. Mycorrhizal status of plant species collected from the Emery coal field.

Plant Species	Mycorrhizal Status[1]
Artemisia bigelovii	+
Atriplex confertifolia	HV
Atriplex cuneata	H
Bouteloua gracilis	+
Chrysothamnus nauseosus	+
Chrysothamnus viscidiflorous	+
Ephedra torreyana	HV
Eriogonum cernuum	-
Eriogonum corymbosum	+
Eriogonum inflatum	-
Eriogonum jamesii	+
Helianthella microcephala	+
Hilaria jamesii	+
Hymenoxys richardsonii	+
Lepidium montanum	-
Leptodactylon pungens	+
Machaeranthera grindelioides	+
Oenothera caespitosa	-
Oenothera pallida	-
Opuntia polyacantha	HV
Oryzopsis hymenoides	+
Sarcobatus vermiculatus	HV
Sphaeralcea coccinea	+
Sporobolus airoides	+
Xanthocephalum sarothrae	+

[1] + = VA mycorrhizae present, arbuscules observed
- = VA mycorrhizae absent
H = Hyphae observed
HV = Hyphae and vesicules observed

Table 3. Mycorrhizal status of plant species collected from Davis Gulch, Colorado.

Plant Species	Mycorrhizal Status[1]
Achillea millefolium	+
Agropyron trachycaulum	+
Androsace septentrionalis	-
Artemisia frigida	+
Artemisia tridentata	+
Astragalus flexuosus	+
Astragalus spatulatus	+
Bromus inermis	+
Carex rossii	-
Chaenactis douglasii	+
Chrysothamnus nauseosus	+
Chrysothamnus viscidiflorus	+
Cleome lutea	-
Cryptantha sericea	+
Descurainia californicum	-
Eriogonum umbellatum	-
Gayophytum rassimossum	-
Gilia aggregata	+
Hordeum jubatum	+
Lappula redowski	+
Lepidium densiflorum	-
Machaeranthera bigelovii	+
Mentzelia dispersa	-
Oenothera caespitosa	-
Oenothera coronopifolia	-
Opuntia polyacantha	-
Oryzopsis hymenoides	+
Oxytropis lambertii	+
Penstemon pachyphyllus	+
Penstemon strictus	+
Phacelia hastata	+
Phacelia splendens	+
Polygonum douglasii	-
Sambucus caerulea	+
Senecio multilobatus	+
Sitanion hystrix	+
Solanum triflorum	-
Sphaeralcea coccinea	+
Stipa comata	+
Tragopogon dubius	+
Verbascum thapsus	+
Xanthocephalum sarothrae	+

[1]+ = VA mycorrhizae present
- = VA mycorrhizae absent

Table 4. Identified species of mycorrhizal fungi.

ALTON COAL FIELD
Glomus constrictus
Glomus macrocarpus[1]
Glomus microcarpus[3]
EMERY COAL FIELD
Acaulospora laevis
Glomus constrictus
Glomus fasciculatus[2,3,4]
Glomus microcarpus[3]
Glomus mosseae[1]
DAVIS GULCH OIL SHALE SITE
Gigaspora calospora[2]
Glomus fasciculatus[2,3,4]
Glomus mosseae[1]

[1]Isolated from coal spoils in New South Wales, Australis (Khan 1978)
[2]Isolated from coal spoils in Scotland (Daft et al 1975)
[3]Isolated from coal spoils in Wyoming (Allen and Allen 1980)
[4]Isolated from coal spoils in Pennsylvania (Daft et al 1975)

Table 5. Soil properties of four treatments to processed oil shale. Study plots are located at Davis Gulch, Colorado.

	pH	ECe[1] mmhos/cm	- - - meq/l - - - Na	Ca + Mg	SAR[2]
Shale					
0-4"	8.3	43.0	230	288	19
4-8"	7.9	21.0	92	125	12
12-16"	7.9	14.0	40	106	5
Rock Mulch					
0-4"	7.9	18.0	80	107	11
4-8"	8.1	43.0	226	284	19
12-16"	8.0	30.0	148	278	16
Topsoil					
0-4"	6.9	0.8	1.2	6.7	0
4-8"	7.4	3.5	8.3	43	2
12-16"	7.8	9.2	31	98	4
Subsoil					
1-12"	7.7	0.4	1.2	3.4	1

[1]Electrical Conductivity

[2]Sodium Adsorption Ratio

Figure 1. Relationship between the percent colonization of host plant roots grown on five soil treatments and the number of days host plants were grown. Confidence interval ± 5%

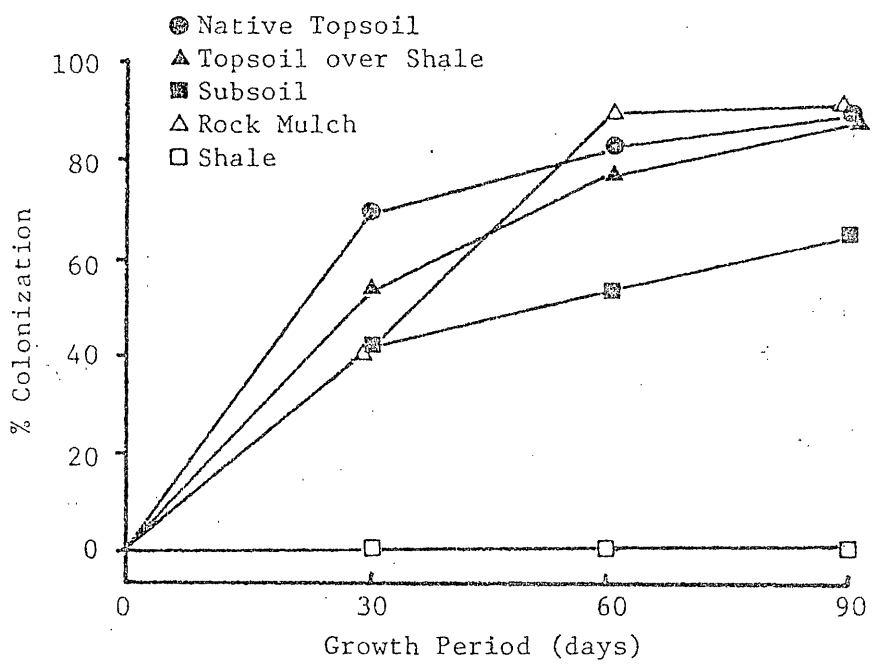
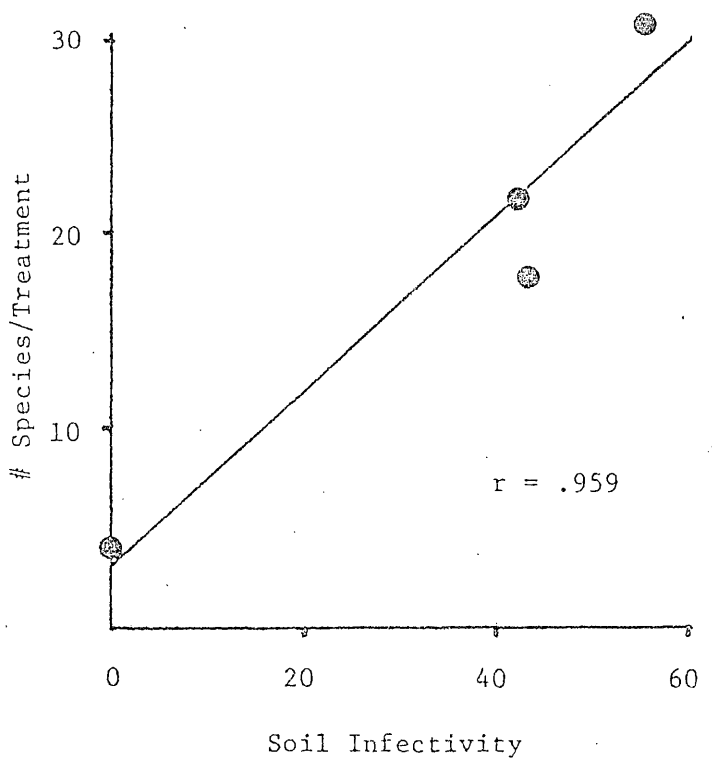


Figure 2. Correlation between soil infectivity and the number of plant species which had invaded onto the soil treatments. Significant at the .025 level.



Appendix 1. Plant species invading onto oil shale treatment plots at Davis Gulch, Colorado.

TOPSOIL OVER SHALE

+ Achillea millefolium
+ Artemisia frigida
+ Artemisia tridentata
+ Astragalus spatulatus
+ Bromus inermis
+ Bromus tectorum
- Carex rossii
+ Chrysothamnus nauseosus
+ Chrysothamnus viscidiflorus
+ Cryptantha sericea
- Eriogomun unbellatum
- Gayophytum racemosum
+ Gilia aggregata
+ Hordeum jubatum
+ Lappula redowski
- Lepidium densiflorum
+ Machaeranthera bigelovii
- Oenothera caespitosa
- Oenothera coronopifolia
- Oenothera pallida
- Opuntia pulyacantha
+ Oryzopsis hymenoides
+ Oxytropis lambertii
+ Penstemon pachyphyllus
+ Penstemon strictus
+ Phacelia hastata
- Polygonum douglassii
+ Sitanion hystrix
+ Tragopogon dubius
+ Verbascum thapsus
+ Xanthocephalum sarothrae

STRAW-MULCHED SHALE

+ Bromus tectorum
- Lepidium densiflorum
- Polygonum douglassii
+ Sitanion hystrix

ROCK MULCH OVER SHALE

+ Achillea millefolium
+ Agropyron trachycaulum
+ Artemisia frigida
+ Astragalus spatulatus
+ Bromus inermis
+ Bromus tectorum
+ Chrysothamnus viscidiflorus
+ Cryptantha sericea
+ Hordeum jubatum
+ Lappula redowski
+ Machaeranthera bigelovii
+ Oryzopsis hymenoides
+ Penstemon pachyphyllus
+ Penstemon strictus
- Polygonum douglassii
+ Senecio multilobatus
+ Sitanion hystrix
+ Verbascum thapsus

SUBSOIL

+ Achillea millefolium
+ Artemisia frigida
+ Artemisia tridentata
+ Astragalus flexuosus
+ Astragalus spatulatus
+ Bromus tectorum
+ Chrysothamnus viscidiflorus
+ Cryptantha sericea
- Descurainia californicum
+ Hordeum jubatum
+ Lappula redowski
+ Machaeranthera bigelovii
+ Oryzopsis hymenoides
+ Penstemon pachyphyllus
+ Penstemon strictus
+ Phacelia hastata
- Polygonum douglassii
- Salsola kali
+ Senecio multilobatus
+ Sitanion hystrix
+ Verbascum thapsus
+ Xanthocephalum sarothrae